Microbial-Faunal Interactions as They Influence Soil Organic Matter Dynamics

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Keywords: microbial/faunal interactions, soil organic matter, crop residues, microbial biomass, water-stable aggregates

Several papers and entire symposia (1,2) have been devoted to the topics of effects of soil fauna on soil structure. Others have addressed the impacts of soil fauna on soil O.M. dynamics (3-5).

From recent studies in both the Netherlands and the USA, we have examined the impacts of primary decomposers, and fauna (microarthropods, earthworms and enchytraeids) on soil organic moieties. Here we contrast the results from Typic Hapludults/Kanudults of the Georgia Piedmont (USA) and a Typic Fluvaquent of one of the recently reclaimed polders of The Netherlands.

A. Relative Importance of Bacteria and Fungi in SOM Dynamics

Several lines of evidence support the hypothesis that fungi are dominant primary decomposers in our Georgia Piedmont no-tillage (NT) systems, 9 years after introduction of the technique (6,7). (1) Fungal hyphal lengths were consistently higher over an annual cycle in surface layers of NT where plant litter is placed on the soil surface, compared to conventional tillage (CT) where litter is buried twice-yearly by plowing to 15 cm. At greater depths hyphal lengths were not different between NT and CT. (2) Studies of microbial activity in litterbags suggested that potentially active fungal biomass is greater in NT-surface litter than CT-buried litter during summer/fall. Active microbial biomass showed a greater fungal than bacterial component in NT-surface litter, but a more equal distribution between the groups in CT-buried litter. (3) Additional studies have explored the effects of fungicide treatments on fungivore fauna, surface and buried litter decomposition and residue N content. The fungicide Captan reduced saprophytic fungal densities by 39-83% and resulted in 27% reduction in NT-surface residue decomposition (Fig. 1). Fungal inhibition also reduced litter N immobilization and resulted in higher C:N

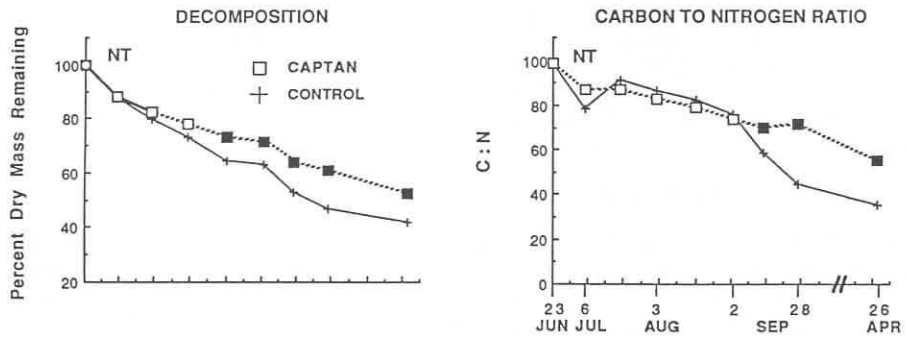


Fig. 1 Percent dry mass remaining and C:N ratios of rye litter in Georgia NT agroecosystem plots. Blackened squares indicate significant differences from control by date.

Table I. Percentage of fungi in total microbial population of minimum tillage (MT) and conventional tillage (CT) sandy loam soil.

March 1987			May 1987		
Horizon (cm)	Field (MT)	(CT)	Horizon (cm)	Field (MT)	(CT)
0-5	13.6	11.1	0-5	10.2	9.0
5-10	12.8	6.3			
10-25	15.1	5.6	15-20	13.2	7.5

Table II. Ratios of several characteristics of a calcareous sandy loam soil under minimum tillage and conventional tillage.

		March	May
soil layer	Total Organic Carbon	1.44	
0-5 cm	Biomass C	1.46	1.14
	Respiration rate	3.23	2.06
	Glucose active biomass	2.31	2.47
	N-flush		2.45
	Nitrogen mineralization rate		2.28
soil layer	Total Organic Carbon	0.93	
15-20 cm	Biomass C	1.28	0.97
or	Respiration rate	0.54	1.17
10-25 cm	Glucose active biomass	0.78	0.85
	N-flush		0.38
	Nitrogen mineralization rate		0.55

ratios (80 vs. 50) during the later stages of surface residue decay. Comparable results were not obtained on buried residues. These findings emphasize the importance of saprophytic fungi to the decomposition and N retention of surface crop residues and as potential links in detrital food webs of no-tillage agroecosystems in Georgia Piedmont soils.

On a marine calcareous sandy loam in The Netherlands, 20 years after the introduction of minimum tillage (5 cm chisel plowing) as opposed to conventional tillage (25 cm moldboard plowing) the microbial population comprised far less fungal biomass C than bacterial biomass C in spring in both CT and minimum tillage (MT) (Table I). Fungal biomass carbon was higher in MT surface soil than in CT sub-surface soil whereas bacterial biomass C was not. Microbial biomass and activity of MT surface soil exceeded those of CT sub-surface soil. Activity parameters (respiration rate with or without added glucose, N mineralization rate) were significantly higher than the relative increases in total organic C and microbial biomass C (Table II). Also, the relative increase of the N-flush was higher than the relative increase in microbial biomass C, indicating a lower C:N ratio of the microbial biomass in MT surface soil. These combined results indicate that in MT surface soil the organic matter is more easily decomposed than in the same layer of CT soil. As expected, opposite results were obtained on CT sub-surface soil.

B. Trophic Groups and Food Web Interactions

Results to date from our field experiments in Georgia do not suggest strong trophic group interactions within the food webs, with the possible exception of fungal- microarthropod interactions. Reductions in microarthropod numbers with naphthalene resulted in increased fungal hyphal length in both CT and NT surface residues on some dates (7). This reflects a tight coupling between the two groups, because of a decline or shift in microarthropod populations in response to significantly reduced fungal abundance in captan treated plots (Fig. 2).

Our limited evidence for trophic group interactions may have been a result of reduced biotic activity during two consecutive years of severe drought. Nonetheless,

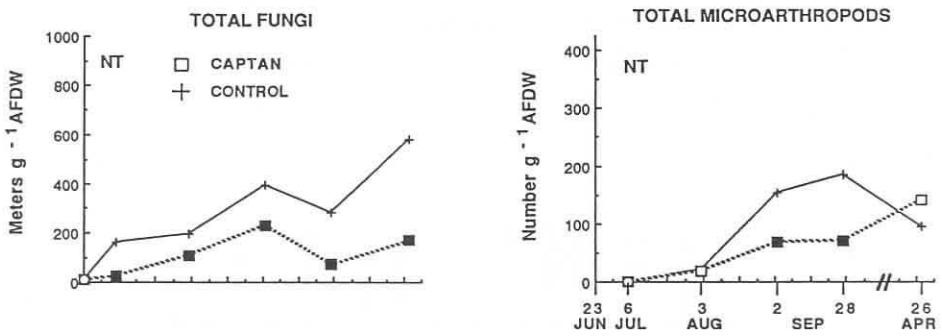


Figure 2 Mean densities of total hyphae and microarthropods in control and captan-treated NT plots. Blackened symbols as in Fig. 1.

we have found that key taxa measurably influence residue decomposition and carbon flux. Total CO_2 output was higher from NT than from CT soils over two annual cycles (8), suggesting greater overall biotic activity in NT soils. Soil fauna (including protozoa) may be responsible for a substantial fraction of this CO_2 output in both NT and CT systems; during their peak of activity, earthworms may account for substantial fractions of heterotrophic respiration in both NT and CT (7,9). Interactions between earthworms and fungi through earthworm casts were assessed in the Dutch soils (see section on soil structure).

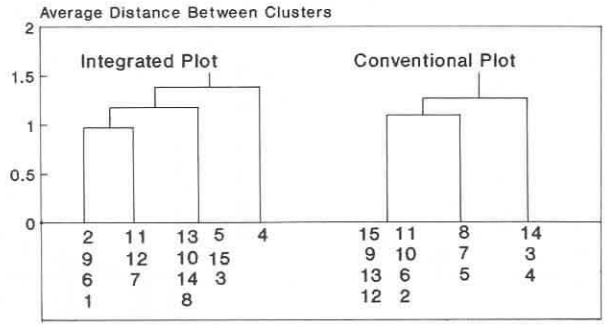
A cluster analysis of our field data in the Netherlands, obtained from plots with integrated management (1.6% organic carbon in topsoil; plow depth 15 cm) and conventional management (1.2% organic carbon in topsoil; plow depth 25 cm) revealed clustering of trophic groups and temporal separation (10) suggestive of food web interactions especially in the integrated treatment (Fig. 3). Bacterial feeders were clustered in one group with bacteria, whereas fungi and fungal feeders were in separate clusters. Predators were scattered over various clusters.

C. Biotic Effects of POM Dynamics

Field studies in Georgia Piedmont agroecosystems (7) have followed changes in microbial and faunal densities and particulate O.M. decomposition using biocides targeted for bacteria (oxytetracycline), saprophytic fungi (captan), microarthropods (naphthalene) and annelids (carbofuran) as compared to untreated controls. The effects of these treatments on end of season coarse (>2.4 mm) and fine particulate O.M. (<2.4,>0.8 mm) standing stocks in no-tillage agroecosystems are shown in fig. 1.

Measurements of unconfined coarse (>2 mm and fine 2-0.8 mm) particulate organic matter (POM) indicate direct biotic effects on litter breakdown (7). Suppression of earthworms and enchytraeids with carbofuran resulted in POM standing stocks 32% higher than controls in NT and 17% higher than controls in CT after 10 months (Fig. 4). Subsequent studies suggested that earthworms and enchytraeids impacted fine POM (2-0.8 mm) more than coarse POM (>2 mm) althought non-target effects of carbofuran on bacteria may have confounded these results (7). We suggest that: (1) fungal reduction with captan slowed the disappearance of POM more in NT than CT, and more in coarse than in fine POM; (2) arthropod reductions with naphthalene slowed coarse POM breakdown in CT and NT; and (3) bacterial reductions with oxy-tetracycline slowed disappearance of fine POM in CT and NT.

In reclaimed polder soil the dispersion index of wet casts of the earthworms Aporrectodea caliginosa was significantly higher ($P<0.001$) than that of artificial casts after 6 and 42 days of ageing. This soil had undergone structure formation for only 45 years, so the relatively thorough moulding inside the worm gut probably caused more dispersion of clay than artificial moulding. Few fungal hyphae developed on both artificial and worm casts, which may have been a result of



1. *Predatory collembola*
2. *Substrate feeding collembola*
3. *Bacteria*
4. *Fungi*
5. *Bacterial feeding mites*
6. *Piercing mites*
7. *Chewing mites*
8. *Nematophgous mites*
9. *Predatory mites*
10. *Bacterial feeding nematodes*
11. *Mycophagous nematodes*
12. *Phytophagous nematodes*
13. *Predatory nematodes*
14. *Amoebae*
15. *Flagellates*

Fig. 3 Clustering and temporal separation of trophic groups in an integrated arable system on a Typic Fluvaquent in the Netherlands. (From: Moore and de Ruiter, in press).

gamma-irradiation as a pre-treatment or the overall low fungal biomass (15% of the total microbial biomass) under natural conditions in this type of soil. Surface related stability significantly ($P<0.02$) increased with age and more so for worm casts than for artificial casts when compared with inside stability, which remained constant. There was no increase in the presence of the fungicide hexanol, indicating the importance of fungi for enhancing the surface stabilty of casts. In preliminary field studies, water stability of air-dried aggregates was not enhanced in worm excrements in the 0.3-1 mm size class as compared to field aggregates of the same size, but in the 1-2 mm size class the percentage water-stable aggregates increased from between 50 and 55% to between 65 and 80%. Under field conditions drying or drying-rewetting cycles appear more important for increasing the stability of earthworm casts than the development of fungi in our soil.

In an Australian duplex soil the development of fungi was relatively more important for stabilizing earthworm casts (11).

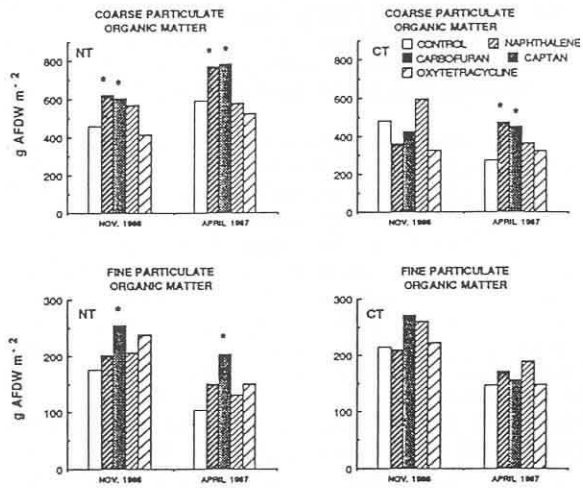


Fig. 4 Standing stocks of coarse and fine POM in 1986 and 1987 in top 15 cm in NT and CT agroecosystems. Asterisks indicate significant differences (P 0.05) across 4 biocides used.

SUMMARY

1. In both Georgia Piedmont and Dutch reclaimed polder soils fungal biomass and microbial activity are higher in NT or MT surface litter or soil than in CT buried litter on sub-surface soil. No generalization can be made as to the absolute importance of biomass and activity of bacteria versus fungi.
2. Resource and food web compartmentation have been shown to promote ecosystem stability (12). To what extent soil tillage and organic residue management interferes with resource and food web compartmentation and ecosystem stability clearly warrants further research.
3. Tillage influenced the breakdown of particulate organic matter by fungi and oligochaetes, both groups showing stronger efffects in NT than in CT. On the other hand, bacterial and arthropod contributions to POM breakdown were similar in both tillage treatments. Differential effects of biotic groups on coarse versus fine POM remain unexplained but may reflect differences in feeding strategies and scales of activity of the organisms.
4. Earthworms may enhance the water-stability of surface casts in structured soil or reduce it in weakly structured soils. Surface fungi developing on casts increase their stability. Drying or drying-rewetting cycles may be more important for stabilizing worm casts than the development of fungi.

REFERENCES

1. Elliott, E.T. and Coleman, D.C. (1988) Let the soil work for us. Ecol. Bulletins, 39, 23-32.
2. Spence, J. (ed.)(1985) Faunal Influences on Soil Structure. Quaest. Entomol., 21,371-700.
3. Mitchell, M.J. and Nakas, J.P. (eds.) (1986) Microfloral and faunal interactions in natural and man-managed ecosystems. Nijhoff/Junk, Dordrecht, Neth.
4. Edwards, C.A., Stinner, B.R., Stinner, D. and Rabatin, S. (eds.) (1988) Biological Interactions in Soil. Agriculture, Ecosystems and Environment, 24,No. 1-3, 380 p.
5. Lavelle, P. (1988) Earthworm activities and the soil system. Biol. Fert. Soils, 6,237-251.
6. Hendrix, P.F., Parmelee, R.W., Crossley, D.A., Jr., Coleman, D.C., Odum, E.P. and Groffman, P.M. (1986) Detritus food webs in conventional and no-tillage agroecosystems. Bioscience, 36,374-380.
7. Beare, M.H., Parmelee, R.W., Hendrix, P.F., Cheng, W., Coleman, D.C. and Crossley, D.A., Jr. (submitted) Biocide manipulations in summer-sorghum conventional and no-tillage agroecosystems: Trophic interactions and system responses to selective inhibition of microflora and fauna. Ecological Monogr.
8. Hendrix, P.F., Han, C. and Croffman, P.M. (1988) Soil respiration in conventional and no-tillage agroecosystems under different winter crop rotations. Soil and Tillage Research, 12,135-148.
9. Hendrix, P.F., Crossley, D.A., Jr., Coleman, D.C., Parmelee, R.W., and Beare, M.H. (1987) Carbon dynamics in soil microbes and fauna in conventional and no-tillage agroecosystems. INTECOL Bulletin, 15,59-63.
10. Moore, J.C. and de Ruiter, P.C. (submitted) Temporal and spatial heterogeneity of trophic interactions within belowground food webs: An analytical approach to understand multi-dimensional systems. Proc. Intl. Wksp. Mod. Tech. in Soil Ecol. Athens, GA Sept. 1989.
11. Marinissen, J.C.V. and Dexter, A.R. (submitted) Mechanisms of stabilization of earthworm casts and artificial casts. Biol. Fertil. Soils.
12. Moore, J.C. and Hunt, H.W. (1988) Resource compartmentation and the stability of real ecosystems. Nature (Lond.), 333,261-263.